

STUDIES OF NEOTROPICAL CADDISFLIES, XXXII:
THE IMMATURE STAGES OF *MACRONEMA VARIIPENNE*
FLINT & BUENO, WITH THE DIVISION OF *MACRONEMA*
BY THE RESURRECTION OF *MACROSTEMUM*
(TRICHOPTERA: HYDROPSYCHIDAE)

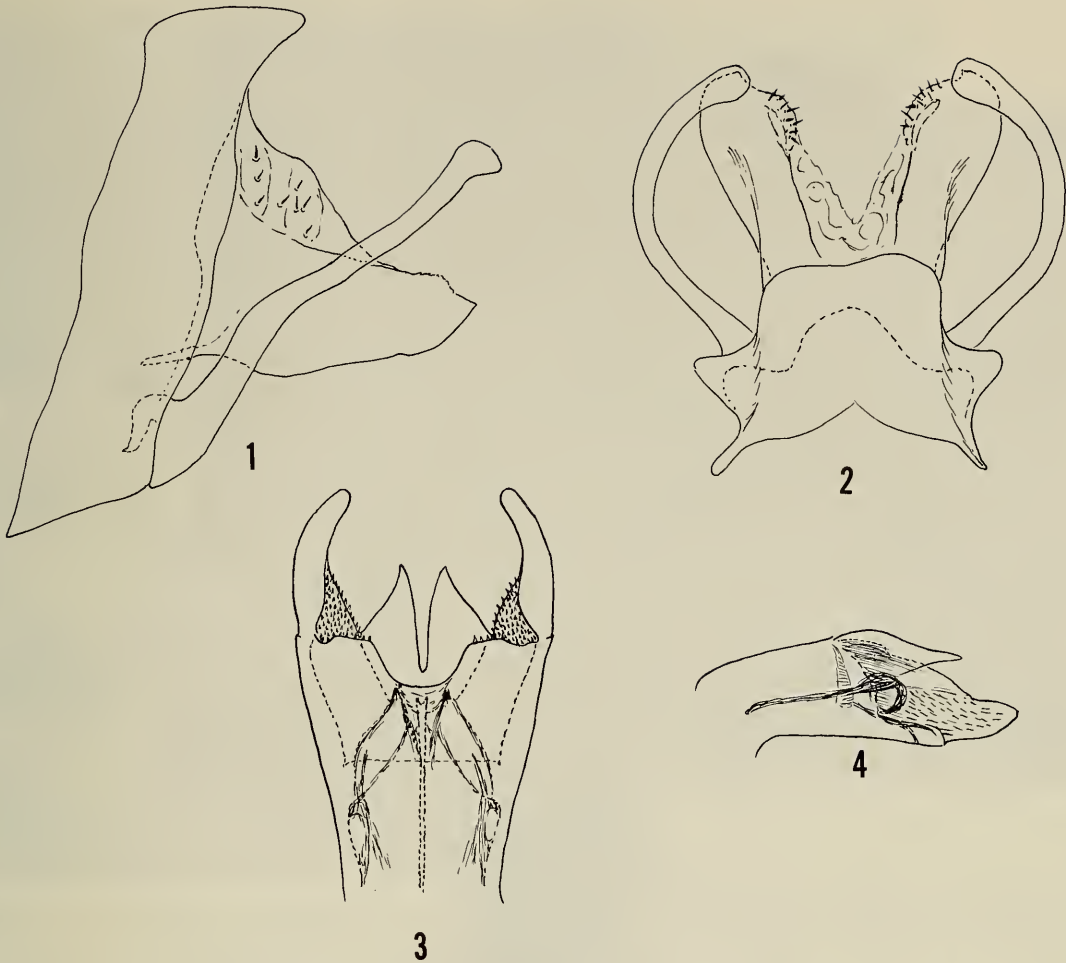
Oliver S. Flint, Jr. and Joaquin Bueno-Soria

Abstract.—The larva and pupa of *Macronema variipenne* are described and figured, and notes on their natural history given. A neotype is established for *M. agnathum* Müller and it and *Leptonema apicale* Navas are synonymized with *M. bicolor* Ulmer, and *M. pullatum* Navas is synonymized with *M. trigramma* Navas. After considering all characteristics of *variipenne* and related species, *Macronema* is divided into two genera: *Macronema* Pictet, with *M. lineatum* Pictet as type, is exclusively Neotropical; and *Macrostemum* Kolenati, with *Macronema hyalinum* Pictet as type, contains not only Neotropical species, but all the species presently assigned to *Macronema* in the Nearctic, Oriental, Ethiopian and Australasian Regions.

The genus *Macronema*, as it has been recognized, is a large genus containing somewhat over 100 described species. The genus is most diverse in the tropics of the New World, Australia, Asia, and Africa, with a few species in North America and northeastern Asia. It is notably absent from Europe and most of northern Asia.

Although many adults have been described, very few larvae have been carefully associated with their adult stage, and most of these are from the northern hemisphere. In spite of the lack of associated material, many larvae of the *Macronematinae* have been described, often incompletely, and then attributed to some genus or species purely on supposition. This has, as one can imagine, produced an extremely confused mess. Ulmer (1957, pp. 332-335) made a heroic attempt to straighten out this confusion, and, in general, succeeded.

He united, under the name of *Centromacronema auripenne* (Ramb.), a series of descriptions of a very distinctive larval and pupal type from South America. This form was first made known through a series of works by Müller (1880, 1881, 1921 and variously referred to as *Macronema*, *Macronema agnathum*, *Macronema* species, third species, species C, and *Macrosterium*), and later fully supplemented by the works of Thienemann (1905 as *Macronema*), Marlier (1964 as *Centromacronema*), Roback (1966 as *Hydropsychidae* sp. 2), and Botosaneanu & Sykora (1973 as *Centromacronema*). This larval type has often appeared in our collections in small numbers, but under circumstances that never permitted a firm association of stages. Finally we realized that these larvae were generally found on plants, often in attached, free-floating roots or leaves, or in and around the roots of emergent plants. With this information, Bueno was able to bring back to the laboratory and rear in an aquarium several adults from a series of these larvae. The adults that emerged turned out to be our recently described species, *Mac-*



Figs. 1-4. *Macronema bicolor*, male: 1, Genitalia, lateral; 2, Same, dorsal; 3, Tip of aedeagus, dorsal; 4, Same, lateral.

ronema variipenne, not a species of *Centromacronema* which also flies on the same stream.

We take this opportunity to describe and figure the larvae and pupae of *variipenne*, select and figure a male neotype of *M. agnathum* Müller, synonymizing it and *Leptonema apicale* Navas with *M. bicolor* Ulmer, and finally to discuss the generic implications of this evidence, restricting *Macronema* to a group of exclusively Neotropical species and resurrecting *Macrostemum* for another group of worldwide distribution.

Macronema bicolor Ulmer

Figs. 1-6

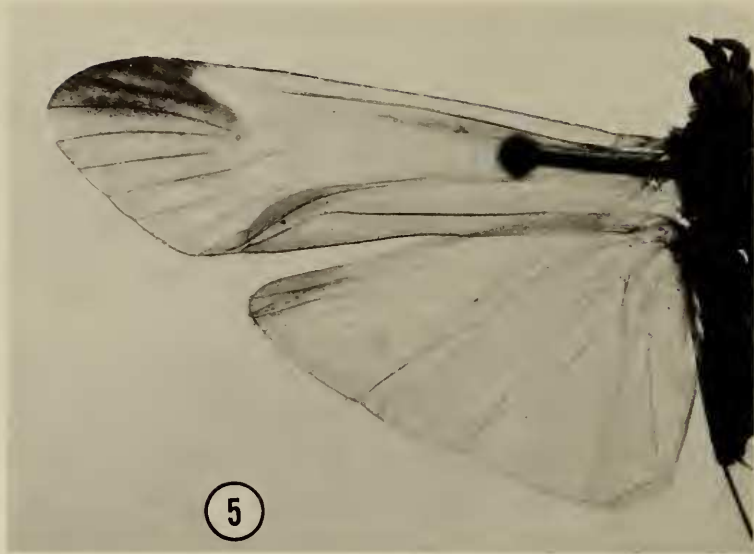
Macronema bicolor Ulmer, 1905a:75. Fischer, 1963:178. Flint, 1966:6.

Macronema agnathum Müller, 1921:530. Ulmer, 1957:338. Fischer, 1963:177.

(New Synonymy)

Leptonema apicale Navas, 1927:40. (New Synonymy)

Because the identity of the larvae described by Müller under the name *Macronema agnathum* has been unknown, and this uncertainty has been in large part responsible for the confusion referred to above, we have made a concerted effort to locate material from Müller. We have located some material in the Museum



Figs. 5-6. *Macronema bicolor*: 5, Wings of lectotype; 6, Wings of neotype of *M. agnathum*.



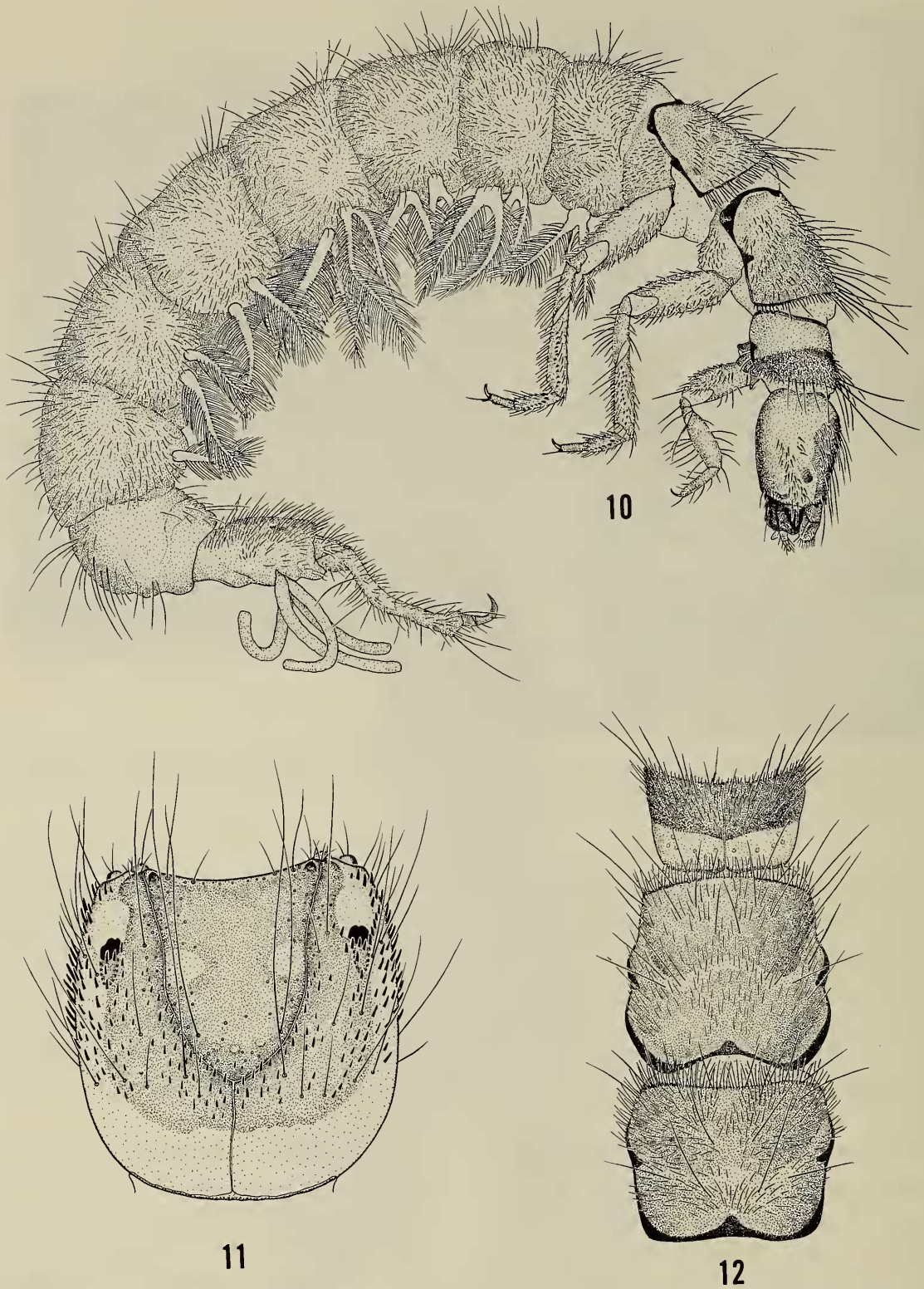
Figs. 7–9. Habitats: 7, Río Palma, above La Palma, Veracruz, Mexico; 8, Marginal vegetation; 9, Aroid plant removed, in whose roots larvae were found.

of Comparative Zoology, Harvard University, and the Natural History Museum, Vienna. In this latter collection are an adult male and female and two pupal skins in excellent condition, all labeled in Müller's hand "Macronema III," and the two adults also "19/8 87." Because the two adults agree with the brief diagnosis, and the pupae are in total agreement with the more extensive description and figures in Müller (1921), and are from him personally, we believe this material to authentically represent Müller's concept of *agnathum* and are therefore labelling the male "Neotype."

The neotype is the same species as *M. bicolor* Ulmer with which it is here synonymized. Ulmer (1957, p. 341) also noted (courtesy of Mr. D. E. Kimmins) that the British Museum (Natural History) had examples labeled "III" and that these too were *bicolor*, but then decided that III referred to *M. chloraemus* Müller, not *agnathum*. It appears that he was confused by the erratic usage of letters, numbers, and names by Müller.

The type male of *Leptonema apicale* Navas located in the Deutsches Entomologisches Institut, Akademie der Landwirtschaftswissenschaften, was borrowed (through the kindness of Dr. G. Petersen) and studied. It is a rather faded example that matches *bicolor* in all respects, with which it is herewith synonymized.

The figures of the male genitalia here presented (Figs. 1–4) were prepared from the neotype of *agnathum*, as is the photograph of the wings (Fig. 6). The neotype

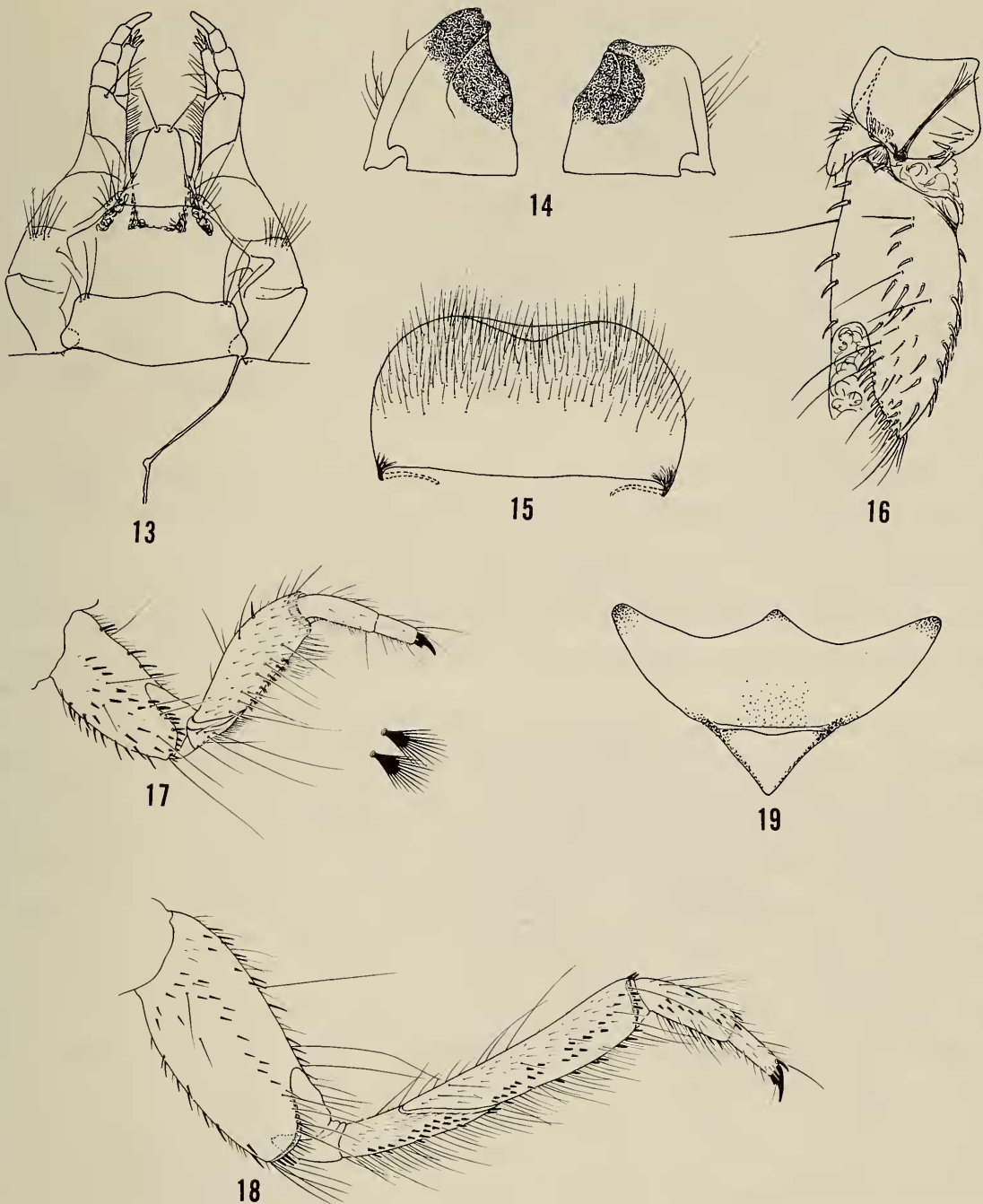


Figs. 10–12. *Macronema variipenne*, larva: 10, Lateral; 11, Head, dorsal; 12, Thorax, dorsal.

is in excellent, unrubbed condition, whereas the types of *bicolor* and *apicale* are rubbed and appear rather different in coloration (Fig. 5).

Macronema variipenne Flint & Bueno
Figs. 7–24

Macronema variipenne Flint & Bueno, 1979:528–532.

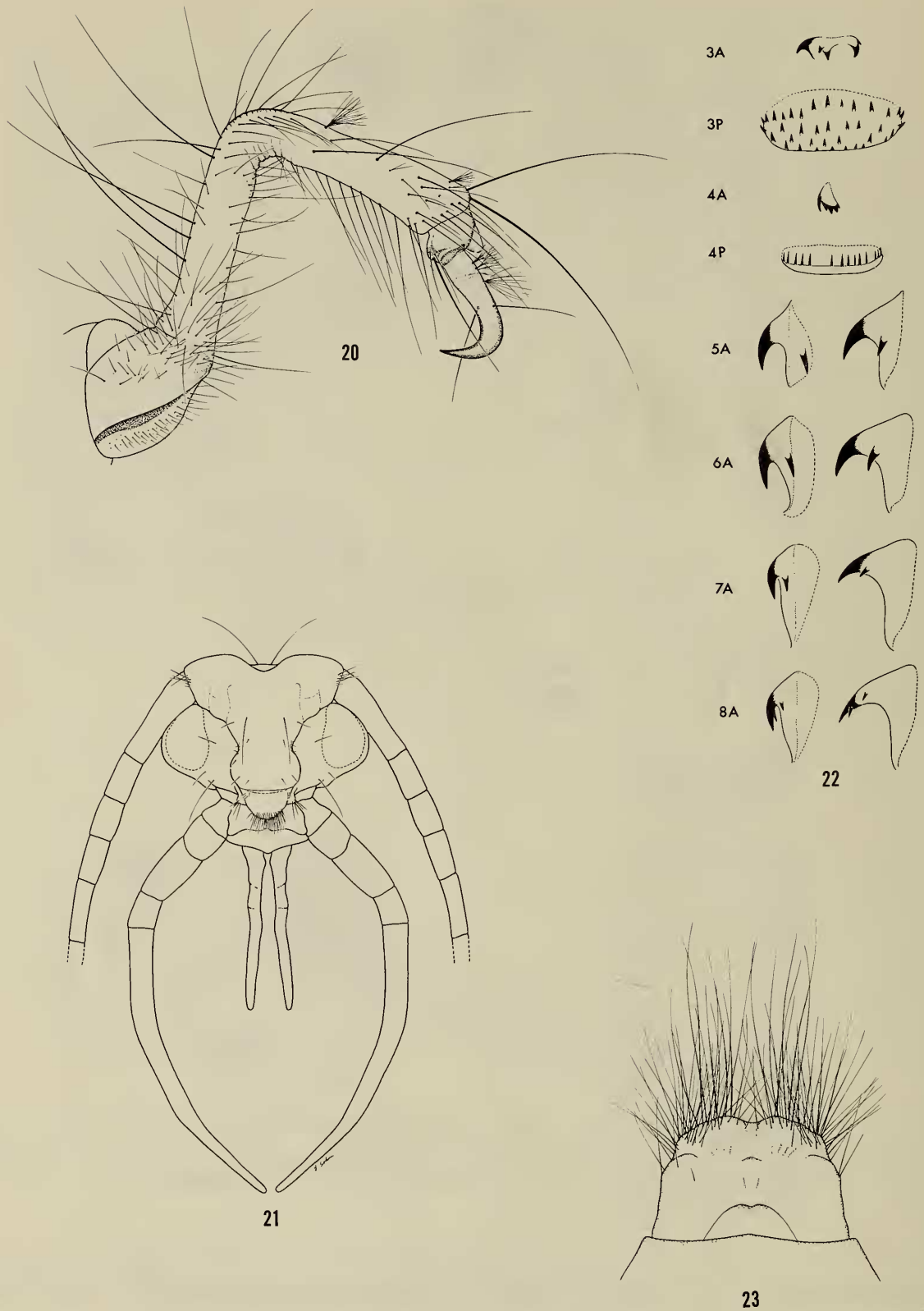


Figs. 13–19. *Macronema variipenne*, larva: 13, Maxillolabium and anterior region of genae, ventral; 14, Mandibles, ventral; 15, Labrum, dorsal; 16, Forepleuron and coxa, lateral; 17, Foreleg, lateral, with 2 margin hairs of femur enlarged; 18, Midleg, lateral; 19, Prosternite, ventral.

This species is widespread through eastern and southern Mexico, south throughout Central and South America at least as far as Ecuador. We have taken adults commonly at lights at night as well as by net during the day.

Larva.—Length to 21 mm, width 2.5 mm. Sclerites mostly golden-yellow with darker brown markings.

Head: As wide as long. Color brown dorsomesally, golden-yellow laterally, posteriorly, and ventrally but becoming darkened ventromesally; frontoclypeus with a pair of pale spots laterally. Frontoclypeus with anterior margin concave, with prominent knobs anterolaterally; surface with only a few setae laterally. Genae with surface smooth, beset with short, bladelike setae in a broad band



Figs. 20–23. *Macronema variipenne*: 20, Larval anal proleg, lateral; 21, Pupal head, anteroventral; 22, Pupal hook plates, with segment number and anterior or posterior positions indicated, plates 5A to 8A shown in dorsal aspect to left, in lateral aspect to right; 23, Apex of pupal abdomen, dorsal.

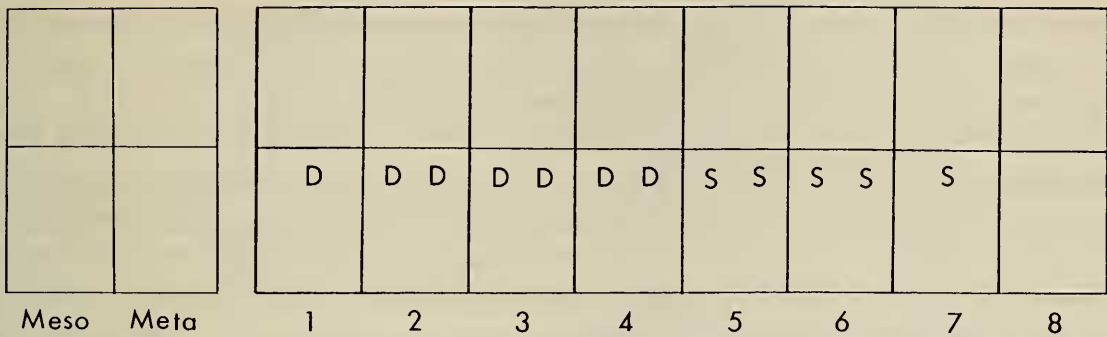


Fig. 24. *Macronema variipenne*, schematic gill diagram of the lateral aspect of the meso- and metathorax and first 8 abdominal segments. S = a single long central stalk with numerous lateral filaments. D = 2 S-type gills arising from a common base.

laterally and posteriorly (but not on pale area posteriorly); with scattered long setae. Genae without stridulatory grooves ventrally; ventral ecdysal line lacking on one side anteriorly, thus anterior ventral apotome is only half delimited. Labrum broad, rounded anterolaterally; anterior half hairy; no anterolateral brushes. Mandibles short, broad, lacking mesal teeth and brushes; apicomeral region strikingly black internally. Submentum with anterior margin convex, with a few setae at anterolateral angles.

Thorax: Pronotum brown on anterior half, yellow on posterior half; meso- and metanota golden-yellow with fuscous lateral and posterior margins. Pronotum with bladelike setae and long hairs on anterior half, posterior half smooth; mesonotum with a few shorter bladelike setae mostly anterolaterally and many long and short hairs; metanotum with only long and short hairs. Prosternite almost crescentic with an anteromesal projection; with a small, triangular sclerite posteromesally. Meso- and metasterna unornamented except for a few short setae. Foretrochantin tapering to a blunt point, with 1 bladelike seta; femur with a ventral row of 8 palmately divided setae; all segments with numerous hairs. Mid- and hindlegs very similar in structure: coxa, femur and trochanter very elongate; trochanter and segments distad, narrow and terete, with rows of short, peglike setae and long and short hairs; tarsus with a single apicodorsal bladelike seta; claw almost straight, with basal setae almost as long as claw. No thoracic gills.

Abdomen: Gills only laterally as shown in Fig. 24. Lateral line lacking. Integument with long and short hairs dorsally, smooth ventrally. Sternum 8 with scattered hairs including 2 pairs of long setae arising from a pair of small, indistinct sclerites. Sternum 9 very hairy, bearing a pair of large, pale, hairy sclerites which also bear a few short, bladelike setae anteriorly; a small narrow sclerite laterad. With 4 long, slender anal gills. Anal prolegs extremely long and slender; ventro-basal plate (attached to the abdomen) bearing a pair of longitudinal dark stripes; legs very long, slender, and hairy with a thin section of cuticle at midlength at which point the legs bend; apical brush reduced to 1 or 2 hairs; claw long, slender, curved.

Pupa.—Length to 10 mm, width 3 mm.

Head: Labrum semicircular, with rounded basolateral lobes; anterior third densely hairy, basolateral angles with 5–6 short setae, basolateral lobes with 5–6 setae. Mandibles membranous, triangular, anterior margin broadly truncate.

Face with a few scattered setae; anterior tentorial pits well marked. Basal antennal segment with a group of setae; antennae very long, curled into several broad loops (not wrapped around the apex of the abdomen).

Thorax: Meso- and metanota with a few scattered setae and a cluster of setae on the tegulae of mesonotum. Midlegs with tibiae and tarsi flattened and fringed.

Abdomen: Segments 3–7 with long, terete lateral processes. Gills laterally between processes and ventrally. Hook plates anteriorly on segments 3–8 (that of 4 very small, those on 5–8 very high); posteriorly on 3 and 4. Segments 3–8 with a few pairs of setae posteriorly. Segments 8 and 9 with a dense fringe of black hairs laterally. No apical appendages, only a cluster of black hairs.

Biology.—The larvae were found in the free-floating mats of roots, and in the tangled roots and stems of emergent plants. The retreats in the root mats were about 30 mm long by 7 mm wide, constructed of fragments of organic matter held together rather loosely by silk and all attached to the rootlets. These retreats were removed as carefully as possible and were preserved promptly, but the larvae generally crawled away quickly. The retreats were later cut open carefully, in an attempt to find some sort of capture net. Nothing of any type could be found, and the retreats seemed to be only a simple tube. We believe that the larvae construct no distinct net, either of the *Macronema* type or of the *Hydropsychinae* type. Perhaps they may construct an irregular mesh of threads outside the shelter, but even that seems unlikely.

Pupal shelters have also been found in the same root mats. These are approximately the same size as the larval shelters, but are a little larger in diameter where the pupa is, and are more firmly constructed. Inside the shelter of silk and detritus, the larva constructs a perfect silken cocoon, free of the outer shelter except near each end. The ends are simply a loose tangle of threads. None of the pupae found in the wild was mature enough to permit species identification.

In order to determine the species of these larvae, Bueno, in the summer of 1978 collected a series of larvae in the Río Palma (Fig. 7), above the village of La Palma. This site is in the tropical wet forest of the coastal lowlands in the state of Veracruz, about 25 km east of Catemaco at an elevation of 30 m above sea level. The river is no more than 15 m wide with an average depth of about $\frac{1}{4}$ m, the water is clear, of good chemical and physical condition, and the bottom is sandy with much gravel and stone. At the sides there are often backwaters with emergent plants, and the marginal trees and vines often put into the water roots which greatly proliferate, frequently forming free-floating mats. The large leaves of the marginal trees and shrubs form a favored resting place for the adults during the day.

The larvae, mostly in the 4th and 5th instars, were collected from the roots and stems of the emergent plants (Figs. 8–9), and then brought back alive to the laboratory in Mexico City, a distance of some 550 km. There they were kept alive in an aquarium in water with sand, sticks and debris all from the Río Palma. The aquarium was of about two liters capacity, and air was supplied by an air pump which at the same time caused the water to circulate in the aquarium. A supply of "Tetramin," a tropical fish food, was circulated with the water every day to provide food for the larvae. When most of the water had evaporated, it was replaced with water directly from the tap.

The larvae mostly disappeared into the bottom sand and debris immediately.

However, a few constructed their retreats on the glass and could be observed in their tunnel. These larvae spent most of their time simply resting in their tube. Rarely they would crawl part way out and appear to be, perhaps, feeding on debris on the retreat. When the water level became low, the current diminished, and they spent much of their time making undulatory movements with the abdomen. After a while these larvae disappeared, and in about 20–30 days adults, which were *M. variipenne*, emerged.

We have examined the gut contents of several field preserved larvae. The guts were filled with rather uniform, roughly cubical, bits of plant tissue about 0.2 mm long on a side.

In summary, it is our belief that the larvae: construct only a rather flimsy, tubular larval retreat without any type of capture net; construct the retreat on plant structures in marginal situations or even buried in silt or sand in backwaters; that they are very tolerant of low water velocities and oxygen concentrations; and that they are “shredders,” biting-out pieces of plant material. The pupae are sheltered in a slightly enlarged and strengthened part of the larval retreat; the pupa is surrounded by a silken cocoon only attached to the outer shelter near the ends; and that the ends of the cocoon are not firmly closed, but loosely plugged by an irregular tangle of silk.

Generic Considerations

Now, with the first unequivocal association of this form of larva with a species of the genus *Macronema*, not *Centromacronema* as it was believed to be (Ulmer 1957; Marlier 1964), the entire question of generic relationships is thrown open.

The descriptions of the immature stages of a number of species of “*Macronema*” have been in the literature for many years: *carolina* Bks. (Ross, 1944), *zebratum* Hag. (Ross, 1944), *transversum* (Walk.) (Ross, 1944), *radiatum* McL. (Lepneva, 1964), *capense* Walk. (Scott, in press), *ulmeri* Bks. (Marlier, 1964, as *siolii*), and others described but not associated with any adult (as listed in Ulmer 1957, pp. 344–345). All these descriptions are very similar and are summarized in Table 1 (under *Macrostemum*) where the contrasting characteristics of *variipenne* are also given (under *Macronema*). I do not believe any trichopterist would consider that such totally discordant characteristics could belong to different species in one genus, especially so if they considered the characteristics of other hydropsychid genera (as shown in Wiggins 1977, for example). No wonder Ulmer (1957, p. 339) concluded that the *variipenne* type larva could not be a *Macronema*, and assigned it to the closely related genus *Centromacronema*.

Unfortunately, we still do not have any larvae definitely correlated with *Centromacronema*, nor with some of the more distinctive species of *Macronema* from eastern Brazil. Such a lack, however, does not affect the problems within *Macronema*, but does prevent a complete solution incorporating all the closely related genera. Recognizing the possibility of the future synonymy of *Centromacronema* with *Macronema*, and the possibility of having to carve more genera from *Macronema*, we will consider the situation within *Macronema*, as these aforementioned possibilities should not affect the stability of the names in consideration.

Ulmer was the first to give notice in a publication (1907) of two distinct groups of species in *Macronema*. The first group of exclusively South American species

Table 1.—Comparisons of certain characters of the larva and pupa of *Macronema* and *Macrostemum*.

	<i>Macronema</i>	<i>Macrostemum</i>
Larva		
Labrum	no brushes	anterolateral brushes
Mandibles	short, no teeth	elongate, toothed
Gena, dorsally	unmodified	with a carina around central area
Gena, ventrally	no stridulatory grooves	with stridulatory grooves
Ventral ecdysal line	lacking on 1 side of pregula	separating pregula on both sides
Coxa	long	short
Foretibia and tarsus	scattered hairs, ventral row of palmate setae	with a large brush of hairs
Mid- and hind tibiae and tarsi	disproportionately short in relation to femur; with rows of short, pointed setae	typical proportions; with ventral rows of feathered setae
Thoracic gills	lacking	present
Abdominal gills	lateral line only	dorsolateral, lateral, and ventrolateral rows
Anal prolegs	very long, jointed in middle	normal, not jointed
Retreat	tubular	branched
Net	none	very regular, of fine mesh
Food	shredders, biting pieces from plant matter	collectors, gathering suspended fine particulate matter
Pupa		
Mandibles	membranous	sclerotized
Labrum	hairy on anterior third	few scattered setae
Antennae	looped only	coiled around abdomen
Posterior hook plates	on segments 3 and 4	on 3 only
Apical appendages	lacking	present
Inner cocoon	free of shelter except at ends	united to shelter
Cocoon ends	loosely plugged	closed

(in which he included *lineatum*, *argentilineatum*, *parvum*, *fulvum*, *bicolor*, and *percitans*) he characterized by a minute discoidal cell, a very large median cell, a distinct, extra, costal crossvein, and the subcostal vein ending on the costa. The other group, consisting of all the other species in the genus, possessed a normal or large discoidal cell, a smaller median cell, no costal crossveins, and the subcosta was united to R_1 just before the wing margin. However, Müller had noticed as early as 1885 (but not published until 1921) a division of the genus based on the presence or absence of the apical tibial spurs on the foreleg and structure of the pupa (as in Table 1). Kolenati (1859) had proposed a new genus *Macrostemum* for *M. hyalinum* Pict. and *M. auripenne* Ramb. based on the absence of such spurs in the latter two species. *M. hyalinum* does have a pair of tibial spurs, but they are very small and easily overlooked in comparison to the large spurs of those species he placed in *Macronema* (*lineatum* although included, was appar-

ently unknown to him). Ulmer in 1957 selected *hyalinum* as the type of *Macrostemum* (but considered it and *Macronema* synonymous), and did correctly attribute the species with the two small spurs to it and the ones lacking spurs to *Macronema*. In 1979 we independently recognized the same two groups on the basis of coloration and male genitalia.

Now with the knowledge of the larval and pupal morphology and ecology, it is obvious that these differences between the two groups of species in the adult stage are much more fundamental. Therefore, we propose to recognize two genera. *Macronema* Pictet (1836) has as its type *M. lineatum* Pictet (monobasic) and in addition contains: *amazonense* Flint, *argentineum* Ulm., *bicolor* Ulm., *bifidum* Flint, *burmeisteri* Bks., *chalybeoides* Ulm., *exophthalmum* Flint, *fragile* Bks., *fraternum* Bks., *fulvum* Ulm., *gundlachi* Bks., *hageni* Bks., *immaculatum* Mos., *lachlani* Bks., *luteipenne* Flint & Bueno, *matthewsi* Flint, *muelleri* Bks., *paliferum* Flint, *parvum* Ulm., *pennyi* Flint, *percitans* Walk., *pertyi* Bks., *picteli* Bks., *reinburgi* Nav., and *variipenne* Flint & Bueno. All species are limited to the Neotropical Realm.

The salient characteristics distinguishing the adults of this genus from *Macrostemum* are: lack of tibial spurs on the forelegs; forewing with Sc ending on the costa; forewing color due mostly to scales, basal $\frac{2}{3}$ usually being green, bounded outwardly by a variably colored area and with costal cell filled with silvery scales; male with claspers undivided or nearly so, tenth tergum shorter and broader, often with lobes and processes, tip of the aedeagus also often bears lobes and processes.

The larval and pupal characteristics are outlined in Table 1.

The second genus is *Macrostemum* Kolenati (1859), with the type *Macronema hyalinum* Pictet (selected by Ulmer 1957). In addition to the type the genus contains the following species in the New World: *arcuatum* Erich., *braueri* Bks., *carolina* Bks., *digramma* McL., *erichsoni* Bks., *maculatum* Perty, *negrense* Flint, *par* Nav., *ramosa* Nav., *santaeritae* Ulm., *subequale* Bks., *surinamense* Flint, *transversum* Walk., *trigramma* Nav. (*pullatum* Nav. is a NEW SYNONYM), *triste* Nav., *tuberosum* Ulm., *ulmeri* Bks., and *zebratum* Hag. In addition, all species listed in the Fischer catalogs (1963, 1972) in *Macronema* from Africa, Asia, and Australia are transferred to *Macrostemum*.

The adults differ from *Macronema* by a combination of the following characteristics: foretibia with 1 or 2 small apical spurs; Sc of forewing united with R_1 apically, or ending in a fork whose ventral arm is united to R_1 and is the stronger of the two arms; forewings with color due primarily to strongly contrasting colors of the membrane and the pattern is widespread over the wing; males with claspers distinctly 2-segmented, the tenth tergum is elongate and rather simple, and the tip of the aedeagus is generally bulbous without special structures.

The larval and pupal structures of this genus are also outlined in Table 1.

Acknowledgments

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